Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data

N. Gayeski, B. McMillan, and P. Trotter

Abstract: We used reported commercial catch data and historical information regarding unreported catches to estimate the abundance of winter steelhead, *Oncorhynchus mykiss*, in Puget Sound rivers in 1895, the year in which the peak commercial catch of steelhead occurred. We employed a Bayesian analysis to address the uncertainties associated with the estimation process and report abundance estimates for four large northern Puget Sound rivers and for the remaining aggregate of rivers and streams in Puget Sound. The central 90% of the posterior distribution of total abundance ranged from 485 000 to 930 000, with a mode of 622 000. Compared with the 25-year average abundance for all of Puget Sound of 22 000 for the 1980–2004 period, our results show that current abundance is likely only 1%–4% of what it was prior to the turn of the 20th century. Loss of freshwater habitat alone can account for this reduction in abundance only if there was an extraordinary decline in productivity. Our estimates of historical abundance should better inform the development of recovery goals for Puget Sound steelhead.

Résumé : Nous utilisons les données des déclarations des pêches commerciales, ainsi que des informations historiques au sujet des récoltes non déclarées, pour estimer l'abondance de la truite arc-en-ciel anadrome, *Oncorhynchus mykiss*, d'hiver dans les rivières de Puget Sound en 1895, l'année durant laquelle s'est produite la pêche commerciale de truites arc-en-ciel anadromes la plus importante. Une analyse bayésienne nous a servi à tenir compte des incertitudes reliées au processus d'estimation et à évaluer l'abondance dans quatre grandes rivières du nord de Puget Sound et pour l'ensemble des autres rivières et ruisseaux de Puget Sound. Les 90 pour cent du centre de la distribution a posteriori de l'abondance totale varient de 485 000 à 930 000, avec un mode à 622 000. Étant donné la moyenne sur 25 ans de l'abondance de 22 000 pour l'ensemble de Puget Sound pour la période 1980–2004, nos résultats montrent que l'abondance actuelle est vraisemblablement seulement de 1%–4% de ce qu'elle était à la fin du dix-neuvième siècle. La perte des habitats d'eau douce par elle-même peut expliquer cette réduction de l'abondance seulement s'il y a eu un déclin extraordinaire de la productivité. Nos estimations de l'abondance dans le passé devraient fournir une base plus solide pour la mise au point de cibles de récupération pour les truites arc-en-ciel anadromes de Puget Sound.

[Traduit par la Rédaction]

Introduction

Steelhead, *Oncorhynchus mykiss*, in the Puget Sound evolutionarily significant unit (ESU) were recently listed as threatened under the US Endangered Species Act (ESA) (Hard et al. 2007; Rausch 2007), prompting the initiation of recovery planning. Recovery planning requires, ultimately, the identification of conditions under which the ESU can be considered to have been recovered and delisted. Prominent among the factors ESA recovery planning must typically address is the rebuilding of population numbers and related life history characteristics such as age and size structure. To this extent, recovery under ESA confronts many of the same problems and controversies that have arisen in discussions of the rebuilding of overfished marine stocks. We agree with Rosenberg et al. (2005, p. 84) that "[i]n the current policy debate about rebuilding depleted fisheries and restoring marine ecosystems, it is important to recognize that fisheries for key commercial species like cod were far more productive in the past. As we attempt to rebuild these fisheries, our decisions should reflect real and realistic goals for management, not just recently observed catch levels."

We believe that the same caution applies to Pacific salmon (*Oncorhynchus* spp.) and steelhead recently listed under the ESA. Whenever possible, recovery planning should endeavor to compare current levels of abundance not only with the levels that immediately preceded ESA listing, but with historical estimates of productivity and abundance as well. Without such an historical perspective, it is impossible to know whether or not recovery targets may underestimate the potential abundance and diversity that is required to assure the persistence of delisted populations.

However, the absence of high-quality quantitative data regarding population abundance and dynamics, of the sort rec-

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ognized today as necessary for proper fish population management, poses a considerable challenge for translating historical information into appropriate quantitative terms. In this paper, we show how several kinds of available historical information for Puget Sound steelhead can be used to estimate historical abundance. We use a Bayesian analysis framework to estimate steelhead run sizes from early records of commercial catch data for the Puget Sound region and other local history sources.

The objectives of this paper are threefold. Our first objective is to provide an evidence-based estimate of steelhead run size in Puget Sound shortly before the turn of the 20th century. While not completely representative of pristine conditions of productivity and abundance of Puget Sound steelhead, estimated abundance at this point in time was considerably greater than the levels that were obtained in the three decades preceding the listing of Puget Sound steelhead in 2007, and together with information on habitat losses, this provides an important perspective on the productive potential of the Puget Sound ESU under current conditions.

Our second objective is to illustrate how quantitative and narrative historical fisheries and socio-economic information can be integrated and employed to obtain credible quantitative estimates of population sizes and conditions that properly acknowledge the uncertainties that are inevitable in such an endeavor. Our third objective is to scale our historical estimates to current and historic estimates of habitat quantity so that our estimates may provide an informative perspective on the productive potential of Puget Sound steelhead under current conditions.

We address the first and second objectives by employing turn-of-the-20th-century (1895) reported commercial catch data for Puget Sound steelhead, along with historical information pertaining to the development of activities resulting in unreported catch of steelhead, to estimate the terminal run sizes of steelhead in Puget Sound. To accomplish our third objective, we employ recent estimates of the amount of habitat in Puget Sound rivers and streams currently available to steelhead as well as estimates of the proportion of steelhead habitat lost since the turn of the 20th century to compare our estimates with current conditions. We then compare both our historic abundance estimates and our habitat-corrected estimates with recent estimates of Puget Sound steelhead run sizes.

To be consistent with the way these early records were compiled, we define the Puget Sound region to include not only the streams draining into Puget Sound itself up to and including the Nooksack River near the Canadian border, but also the streams discharging into Hood Canal and the Washington side of the Strait of Juan de Fuca westward to (but not including) the Makah Indian Reservation. Some streams in this region host two races of steelhead, commonly referred to as winter-run and summer-run, owing to the timing of their entry into their natal streams and their state of sexual maturity when they do so. We limited our analysis to the winter run because, again, the earliest available written records are from fisheries that operated in winter specifically to harvest these steelhead (Collins 1892; Wilcox 1898; Rathbun 1900).

Materials and methods

Sources of historical data

Our source of historical winter steelhead harvest information was a series of reports on commercial harvest in west coast fisheries published by the old US Commission of Fish and Fisheries (Collins 1892; Wilcox 1895, 1898, 1902, 1906; Rathbun 1900; Cobb 1911, 1917, 1921, 1931). The first commercial harvest records for steelhead in Washington date from 1889, the year of statehood (Collins 1892). Commercial fishing in Puget Sound streams is known to have begun much earlier, with American settlers on the Puyallup and Duwamish rivers in 1853 (Anonymous 1853; Morgan 1951), and even prior to that, salmon and steelhead occasionally were accepted in trade at the Hudson Bay Company's Fort Nisqually for consumption at the post (Journal of Occurrences at Nisqually House 1833; Carpenter 1986). But while commercial fishing grew and shifted to other streams in the years following, catch records for this activity went unreported until 1889 (Collins 1892). The reported commercial harvest of steelhead in the Puget Sound region showed a growing trend over the first three periods of actual record, with the peak of reported commercial harvest occurring in 1895 (Wilcox 1898), after which steelhead catches declined (Rathbun 1900; Wilcox 1902, 1906; Cobb 1911, 1917, 1921, 1931), even though commercial effort to catch them did not, so we selected that data set for our analysis. The 1895 data likely reflect the abundance of Puget Sound steelhead populations in the late 19th century immediately preceding the buildup of a directed commercial fishery and, therefore, provides the best quantitative data from which to estimate the abundance of these populations. This follows the lead of the Biological Review Team of NOAA Fisheries, who likewise restricted its own examination of the historical record to the same 1895 data set when it updated its status review of Puget Sound steelhead for the Endangered Species Act (Biological Review Team 2005).

In addition to listing the total commercial catch of steelhead for the Puget Sound region as a whole, the Wilcox (1898) report also listed river-by-river commercial catches for four individual Puget Sound streams in 1895: the Nooksack, Skagit, Stillaguamish, and Snohomish rivers. We augmented this data set with information about the pace and extent of settlement and development from local history sources, including Immigration Society of North-Western Washington (1880), Local Committee of Pioneers (1906), Smith and Anderson (1921), Jeffcott (1949), Edson (1968), Bacon (1970), Clark (1970), Strickland (1984), and White (1992).

Although this data set gave us a solid basis for determining the commercial harvest level for steelhead at its historical peak, it did not include tribal subsistence catches (White 1992), nor did it include catches by "ranchers" for home uses, which, according to Wilcox (1898), were substantial in the aggregate and probably the equal of the commercial harvest. We could find no information regarding sport fishing for steelhead during this period. We accounted for the uncertainty associated with all of this off-the-books harvest as well as certain other uncertainties associated with this historical data set through the use of Bayesian estimation methods as described below. All catch data in Wilcox

(1898) were reported in pounds of fish, not numbers of fish. We inserted the data as reported (in pounds; 1 pound = 0.453 kg) and allowed our algorithms to make the appropriate conversions to numbers of fish.

Bayesian estimation of historical run sizes

For the four individual Puget Sound rivers singled out in the Wilcox (1898) report, and for the remaining rivers and streams in the Puget Sound region overall, we used a Bayesian analysis framework to estimate steelhead run sizes from the reported commercial catch data. The Bayesian approach typically treats the data as fixed (known) and the parameter of interest (in our case, the total steelhead run size, N) as unknown and conducts an inference on N by assuming a process involving N by which the data are generated. The hypothesized process is expressed in an equation known as the likelihood. Distributions (typically called "prior distributions" or "priors" for short) are specified for the unknown parameters of the likelihood, including N itself. The inference from the data via the likelihood produces a (posterior) probability distribution for N. In our case, in addition to the reported commercial catch data, our estimates depend on three unknown parameters: (*i*) the total steelhead catch that was unreported or otherwise not included in the reported commercial catch; (*ii*) the average mass of the steelhead caught; and (*iii*) the harvest rate on the total run that produced the total catch. Although we could not identify definitive point estimates for any of these three parameters, we were able to identify reasonable limits within which their true values are most likely to lie. Thus, we could delimit the extent of the uncertainties of the estimates of these parameters and employ them in our Bayesian analysis framework.

We chose the binomial likelihood on which to base our inference, where T (total catch) $\sim$ Bin(N, R), R being the harvest rate. Thus, we view the catch data as resulting from a binomial sampling of the total run N, at an average harvest rate R, as expressed by this likelihood equation:

$$(1) \qquad P(T|N,R) = \binom{N}{T} \cdot T^R \cdot (N-T)^{(1-R)}$$

where N is total run size, T is total catch in numbers of fish, and R is harvest rate.

The Bayesian inference proceeds by specifying appropriate (prior) distributions for R and N. To employ this approach, however, we first had to expand the reported commercial catch, C, to arrive at an estimate of T. This was done as follows. The reported commercial catch C was multiplied by a quantity U that represents the ratio of unreported catch to reported commercial catch to arrive at a figure for the unreported catch (in pounds). This number was then added to the reported catch to derive a number for the total catch (in pounds). Next, the total catch was divided by the average mass (in pounds) of the steelhead caught, M, to attain a figure for T. Thus:

$$(2) \qquad T = (C + C \cdot U), \text{ or equivalently}, T = C \cdot (1+U)/M$$

where T is total numbers caught, C is the reported commercial catch, U is the ratio of unreported catch to reported commercial catch, and M is the average weight of steelhead caught (in pounds).

However, the only firm figure in eq. 2 is C. Uncertainty surrounds the values of U and M. These uncertainties required that we place distributions on both U and M and repeatedly apply the algorithm to arrive at a value for T (eq. 2) by drawing different values of U and M from the respective distributions. Consequently, we were required to generate a distribution of values of T for each value of C reported for each of the five populations (four rivers and the remaining aggregate of Puget Sound rivers and streams). Thus, our Bayesian analysis is somewhat atypical in that our inference on N is conducted on values of T that are themselves uncertain and consequently are represented by a distribution (the distribution of T). Note also that since the estimation process evaluates the likelihood of each value of N drawn from the prior on N for a large random sample of values drawn from the prior on R and the distribution of T, the posterior distribution of N will be distributed as a beta binomial rather than as a simple binomial, and thus the variance will be much broader than expected under a simple binomial.

All calculations and the inference on N were programmed and carried out using the Fortran shell program SWL (sampling weighted likelihood; written by Daniel Goodman, Environmental Statistics Group, Department of Biology, Montana State University, Bozeman, Montana). SWL samples the prior distributions by direct simulation with calls to random number generators and then weights each sampled set of values of parameters by their likelihood, cumulating histograms and posterior summaries of the sampled parameter values weighted accordingly. This contrasts with sampling or resampling the joint posterior as Markov chain Monte Carlo approaches do. This is extremely efficient for calculations of low dimension (four or fewer parameters) as is the case here with four unknown parameters: N, R, U, and M. This efficiency enabled us to employ ten million samples of all prior distributions and to calculate the posterior distributions of all quantities of interest from these samples using little computer time. We chose uniform distributions for the unknown parameters N, R, U, and M, with upper and lower limits selected on biological and historical grounds to bracket the most likely range within which the true parameter values lie (listed in Table 1).

For each of the five populations, random values of N, R, U, and M were drawn from the respective prior distributions, and eq. 2 applied to the values of U, M, and the population-specific value of C (in pounds) to generate a sample value of T. A posterior value of N was then obtained by calculating the likelihood of N (eq. 1) from the values of N, R, and the derived sample value of T (details of the calculation are described in further detail in Appendix A). By sampling 10 000 000 random combinations of N, R, U, and M, we were assured of adequately sampling the joint parameter space. To improve efficiency, we included a trap that redrew random values of U and M when any derived value of T was larger than the value of N drawn from the prior on N.

For reporting and histogram display of the posterior probabilities, the intervals spanned by the prior probabilities were divided into 100 equal-sized bins. This enabled us to display histogram outputs as smooth continuous curves and to evaluate the probabilities of narrow ranges of parameter values. We examined posterior histograms and related sum-

Table 1. Reported commercial catch for 1895, estimated currently (SC) and maximum historically (SH) accessible stream lengths (km), and prior distributions.

Population	*C*	SC (SH)	*M*-LO	*M*-HI	*U*-LO	*U*-HI	*R*-LO	*R*-HI	*N*-LO	*N*-HI
Nooksack	660 160	612 (918)	7.0	9.5	0.10	0.30	0.60	0.90	80 000	225 000
Skagit	205 190	982 (1473)	7.0	9.5	0.50	1.0	0.30	0.60	50 000	200 000
Stillaguamish	180 000	445 (667.5)	7.0	9.5	0.50	1.0	0.40	0.70	40 000	130 000
Snohomish	401 620	926 (1389)	7.0	9.5	0.50	1.0	0.40	0.70	90 000	290 000
Remainder	518 582	4014 (6021)	7.0	9.5	0.50	1.0	0.40	0.70	100 000	370 000

Note: *C*, reported commercial catch (pounds; 1 pound = 0.453 kg); *M*-LO and *M*-HI, average low and high masses of steelhead caught (pounds); *U*-LO and *U*-HI, low and high ratios of unreported catch to reported commercial catch; *R*-LO and *R*-HI, low and high harvest rates; *N*-LO and *N*-HI, low and high numbers of fish (i.e., run size).

maries of marginal parameter probabilities for total run size, *N*, numerical catch, *T*, and harvest rate, *R*.

Justification of the prior distributions

The limits placed on the priors of all unknown parameters are listed, as well as the specific values of the total reported 1895 commercial catch (in pounds) and the estimated value of currently accessible stream length for each of the four reported rivers and for the remainder of Puget Sound rivers and streams (Table 1).

The distribution of average steelhead mass, M

Steelhead returning to Puget Sound rivers and streams can range from 1.5 pounds to well over 15 or 16 pounds; however, data on numbers and total mass of commercially caught steelhead reported by the Washington State fish commissioner in 1892 yielded an average mass of 8 pounds per steelhead (Crawford 1892). Also, data developed in the 1940s and 1950s for returns to several individual rivers yielded average masses ranging from 7.0 to 9.4 pounds (e.g., Meigs and Pautzke 1941; Larson and Ward 1955; Withler 1966). Therefore, we reasoned that the true average mass of steelhead for the aggregate of Puget Sound rivers and streams should fall within limits of 7.0 and 9.5 pounds.

There is evidence that fishing with gill nets, as was practiced by Native American subsistence fishermen and later by Puget Sound's commercial fishermen, may selectively capture the larger fish in an annual run, thereby exerting a selective pressure for smaller average size in subsequent returns (Hard et al. 2008). Although it could be argued that tribal and commercial fishing could have produced such a result by the time the studies we relied on for our limits on the prior for *M* were undertaken, observations in the zoological report of the Pacific railroad survey of 1853–1855, compiled before commercial fishing got under way to any major extent, indicate that this was not the case for Puget Sound steelhead (Suckley 1860); average sizes and masses appeared to be about the same then as prevailed during the 1940s and 1950s.

The prior on harvest rate R *and the distribution of unreported/reported catch* U

The 1895 commercial catch was the largest catch of Puget Sound winter-run steelhead in the record for the period 1889–1915, culminating the period of rapid buildup of the commercial fishery following statehood in 1889 (e.g., Collins 1892; Wilcox 1898; Cobb 1917). Of the four northern Puget Sound rivers of our primary examination, the commercial fishery on the Nooksack was the most intense and well-developed due in large part to the earlier and sustained industrial development of Bellingham, Washington, which was the commercial heart of the young state north of Seattle until Everett became a sustainable industrial site after 1895 (e.g., Bacon 1970; Clark 1970; Edson 1968). For the same reasons that led to the commercial–industrial development of Bellingham, agricultural settlement of the Nooksack basin by Euro-Americans lagged well behind that on the Skagit, Stillaguamish, Snohomish, and other smaller rivers basins in central and south Puget Sound (cf. Jeffcott 1949). Relative to the size of the Nooksack basin, the commercial catch alone was particularly large, greatly exceeding not only the catch on the other three large rivers but the catch from all remaining rivers in Puget Sound combined (Table 1).

Given the intensity of the commercial fishery and the relative magnitude of the 1895 catch, we determined that the unreported Nooksack catch most likely accounted for a relatively small proportion of the total catch compared with the other rivers. Historic accounts indicate unreported catch was particularly related to agricultural use of anadromous fish runs as fertilizer and livestock feed as well as rural subsistence (Local Committee of Pioneers 1906; Jeffcott 1949; White 1992). We estimated that it was, nonetheless, at least 10% of the reported Nooksack commercial catch but unlikely to have been any greater than 30%, and so bounded *U* by 0.1 and 0.3.

Taking into account both reported and unreported catches, we estimated that the total harvest rate on the Nooksack run was likely to have been particularly high. Specifically, we estimated that the total harvest rate could not have been lower than 60% but was unlikely to have been higher than 90%. So we bounded the prior for the Nooksack between these values.

The commercial fishery on the Skagit was the last to develop among the large river basins in Puget Sound, with fishermen just beginning to learn the run timings during the first 1895 reported catch period (Wilcox 1898). The nonreported catch related to agricultural use, in particular, was of great magnitude (Local Committee of Pioneers 1906; White 1992), probably equaling the commercial catch as reported for steelhead in 1895 on the Stillaguamish River (Wilcox 1898). We therefore chose to bound *U* for the Skagit and for all other rivers by 0.5 and 1.0. In other words, we assume that the unreported catch in these rivers was at least half of the reported commercial catch, and Wilcox (1898) states "probably" equaled it. Despite the relatively undeveloped state of the commercial fishery on Skagit steelhead, the reported catch was still considerable (Table 1), but in view of the size of the basin, we estimated that the total harvest rate was likely lower than on the Nooksack, perhaps as low as 30%, but no greater than 60%.

The Stillaguamish and Snohomish river basins were both closer to developing commercial centers in Everett and Seattle (Wilcox 1898; Clark 1970) than the Skagit but also had considerable agricultural development with related unreported catch probably high (e.g., Wilcox 1898; Local Committee of Pioneers 1906; White 1992). The reported commercial harvest from both rivers was nearly proportional to estimated accessible stream lengths in each basin (SH, Table 1) and greater than that in the Skagit but much less than that in the Nooksack. We therefore estimated that the total harvest rate was unlikely to be lower than 40% but no greater than 70%.

Most of the rivers and streams comprising the remaining Puget Sound steelhead populations were individually smaller than the Skagit or Snohomish and were likely of variable productivity. Most had likely experienced early levels of settlement and agricultural development comparable to the Skagit, Stillaguamish, and Snohomish (e.g., Local Committee of Pioneers 1906; Edson 1968; Steilacoom Historical Museum Association 2009), so we assumed that the total of the unreported catch bore a similar proportion to the reported catch as in the larger rivers. Thus, we bounded U between 0.5 and 1.0 as for the others. We also assumed that the total harvest pressure was comparable to that estimated for the Stillaguamish and Snohomish, and so bounded R between 0.4 and 0.7. This assumption is particularly conservative given that the reported commercial catch is substantially smaller relative to total accessible stream length (Table 1). Lower harvest rates would result in larger posterior estimates of total run size than those we arrived at. As previously noted, we found no information concerning the magnitude of sport fishing for steelhead during this period. The fact that it escaped mention in the numerous historical sources we did consult suggests that sport fishing during this period constituted a small fraction of the off-the-books steelhead catch. If major sport fishing catch did occur in any of the Puget Sound rivers, our failure to include it in the analyses would only have the effect of further underestimating U and thus the total catch T. The magnitude of the resulting underestimation of T is unlikely to be considerable enough to affect the range of the priors on R, and thus we believe the net effect would be to underestimate the run sizes.

Distributions for run size, N

No information was available that would have permitted us to estimate an informative unimodal or multimodal prior distribution for N for any of the four rivers or the remainder of Puget Sound. We therefore chose uniform distributions with lower limits slightly less than the lowest values of T, knowing that the estimation algorithm would exclude values less than T as explained above. Upper limits on N were chosen by trial and error to provide limits slightly larger than the largest value of N in the posterior distribution. In this way we allowed the likelihood to entirely dominate the calculation of the posterior distribution, in keeping with the intention that the priors for N be uninformative. This approach will have the effect of inflating the posterior variance of N compared with a case in which an independent prior is chosen such that a portion of the posterior probability mass is constrained to “pile up” at the upper or lower boundaries of the prior.

Comparison of historical with contemporary run size

To compare our estimates of 1895 run sizes with current conditions, we used NOAA Fisheries’ estimates of recent average abundances presented in the 2005 Status Review of Puget Sound Steelhead (Biological Review Team 2005, their table 5). This table presents run size estimates averaged for all years between 1980 and 2004 for which data were available, and for the most recent 5 years prior to the date of the review (2000–2004), for all rivers except the Nooksack. The only recent run size data available for the Nooksack is from the 2003–2004 return year when 1598 wild steelhead returned (WDFW 2006). We rounded this to 1600 and used this number for both the 25- and 5-year averages for the Nooksack. These contemporary run sizes are presented for the five populations for which we provided estimates of 1895 run size (Table 2).

To further facilitate comparison and interpretation of these numbers, we translated them into fish-per-accessible-stream-kilometre (FKM) using recent NOAA Fisheries estimates of stream lengths within river basins that are currently accessible to returning adult steelhead (D. Holzer, NOAA–NMFS Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, USA, personal communication, 2009; cf. also Beechie et al. 2001). Based on additional discussions with NOAA staff (D. Holzer and T. Beechie, personal communications, 2009, 2010), we estimated that the maximum proportion of habitat accessible to steelhead in any river basin in 1895 that has been lost during the 20th century is 33% (that is, we estimate that currently accessible stream lengths are two-thirds the total lengths available in 1895). Washington Department of Fish and Wildlife recently estimated the percentage of winter steelhead stream habitat lost in Puget Sound during the 20th century to be 21% (Scott and Gill 2008). We chose the larger NOAA estimate as being more conservative and used this larger habitat loss figure to estimate the maximum length of stream kilometres (SH) accessible to steelhead in 1895. Thus, we multiplied current accessible stream lengths (SC in Table 1) by 1.5 to generate estimates of SH for each of the five populations (SH in Table 1). We then divided the posterior mode and posterior 5th-percentile estimates of N by the SH value for each population to produce modal and 5th-percentile posterior estimates of FKM (Table 3). We also divided the two mean run size estimates of the same populations under current conditions by the SC value for each to produce estimates of FKM for the 1980–2004 and 2000–2004 averages (Table 2).

Results

Estimates of historical catch (T), harvest rates (R), and run sizes (N)

The posterior distribution of the parameter N, the distribution of T, and the posterior distribution of the parameter R for the Snohomish River basin are displayed (Figs. 1–3).

These distributions are representative of the shapes of the

Table 2. Puget Sound (PS) steelhead run sizes from NOAA Fisheries 2005 Status Review.

	N			FKM	
Population	1980–2004	2000–2004	SC	All years	5 years
Nooksack*	1 600	1 600	612	2.6	2.6
Skagit	6 993.9	5 418.8	982	7.12	5.52
Snohomish	5 283	3 230.1	926	5.71	3.49
Stillaguamish	1 027.7	550.2	445	2.31	1.24
Rest of PS	6 673.8	4 742.5	4 014	1.69	1.18
All of PS	21 678	1 5542	6 979	3.1	2.2

Note: *N*, average wild run sizes for 1980–2004 and for 2000–2004; SC, current estimates of accessible stream lengths; FKM, equivalent fish-per-accessible-stream-kilometre.

*Data for 2003–2004 from page 18 of the appendix "Puget_snd_esu" in Scott and Gill (2008).

Table 3. Estimated 1895 Puget Sound (PS) steelhead abundance (*N*), estimates of historically accessible stream lengths (SH), and equivalent fish-per-accessible-stream-kilometre (FKM).

Population	Posterior mode *N*	Posterior 5th percentile *N*	SH	FKM, mode *N*	FKM, 5th percentile *N*
Nooksack	127 800	101 400	918	139	110
Skagit	86 700	70 000	1 473	59	48
Snohomish	153 000	114 000	1 389	110	82
Stillaguamish	69 200	51 700	667.5	104	77
Rest of PS	185 000	148 000	6 021	31	25
All of PS	621 700	485 100	10 469	59.4	46.3

Fig. 1. Posterior distribution of total steelhead run, *N*, for the Snohomish River in 1895: (mean = 164 500; mode = 153 000; standard deviation = 33 400; central 90% of the posterior distribution: 114 000–224 000).

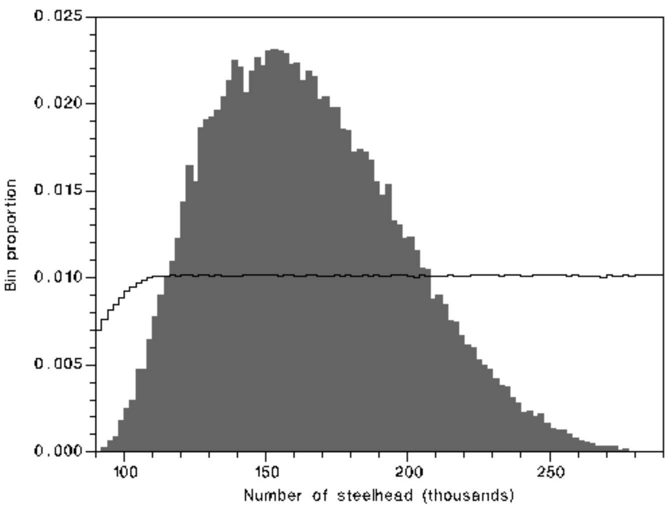
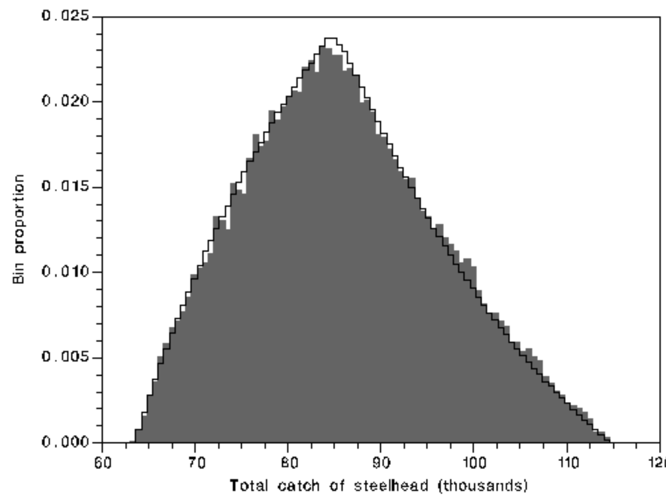


Fig. 2. Distribution of the total numerical catch of steelhead, *T*, for the Snohomish River in 1895: (mean = 85 900; mode = 83 700; standard deviation = 10 400; central 90% of the distribution: 69 500–104 300).



distributions of these parameters for all five populations. For the parameters *N* and *R*, the priors are overlaid on the posteriors as thin lines. The mean, mode, standard deviation, and central 90% of these distributions are listed (Table 4). In addition, the sums of these quantities for *N* and *T* are shown. For *R*, the mean values are shown. These latter quantities were calculated in two ways: (*i*) as grand means of the individual population mean values and (*ii*) directly from the totals for *N* and *T*.

The posterior distribution of *N* and the distribution of *T* for all five populations are essentially normal. This is expected given the uniform priors employed. The shape of the distribution of *T* results from the uniform distributions for *U* and *M* employed in eq. 2. Given normal distribution of the data, the near-normality of binomial distributions for large sample size, and appropriately broad uniform priors on *R* and *N*, near-normality in the posterior of *N* is expected. In all five cases, the posterior is shrunk considerably from the lower and upper limits of the uniform prior.

Fig. 3. Posterior distribution of the total harvest rate, *R*, for the Snohomish River in 1895: (mean = 0.54; mode = 0.42; standard deviation = 0.087; central 90% of the posterior distribution: 0.41–0.68).

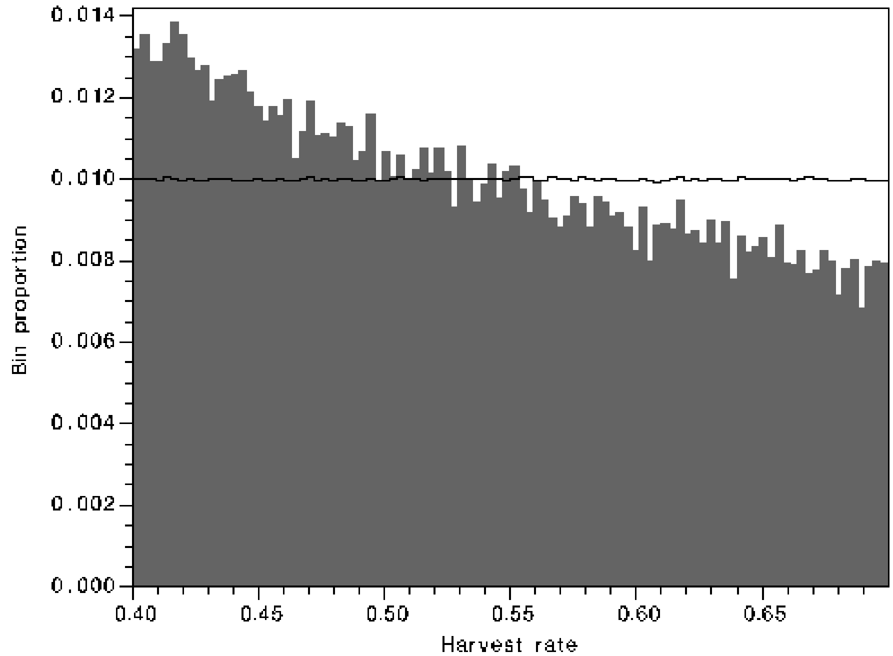


Table 4. Posterior parameter distributions and the distribution of total numbers caught.

Population, parameter	Mean	Mode	Standard deviation	Central 90%
Nooksack run size, *N*	132 600	127 800	20 400	101 400–169 000
Skagit run size, *N*	105 600	86 700	24 700	70 000–149 000
Snohomish run size, *N*	164 500	153 000	33 400	114 000–224 000
Stillaguamish run size, *N*	73 700	69 200	14 900	51 700–100 000
Rest of PS run size, *N*	212 100	185 000	43 100	148 000–287 700
Totals	688 500	621 700	136 500	485 100–929 700
Nooksack total catch, *T*	96 800	91 300	9 700	81 700–113 500
Skagit total catch, *T*	43 900	43 300	5 300	35 000–53 100
Snohomish total catch, *T*	85 900	83 700	10 400	69 500–104 300
Stillaguamish total catch, *T*	38 500	37 700	4 700	31 100–46 600
Rest of PS total catch, *T*	110 800	109 000	13 500	89 400–134 500
Totals	375 900	365 000	43 600	306 700–452 000
Nooksack harvest rate, *R*	0.74	0.60	0.09	0.61–0.88
Skagit harvest rate, *R*	0.43	0.31	0.09	0.31–0.58
Snohomish harvest rate, *R*	0.54	0.42	0.09	0.41–0.68
Stillaguamish harvest rate, *R*	0.54	0.42	0.09	0.41–0.68
Rest of PS harvest rate, *R*	0.54	0.40	0.09	0.41–0.68
Grand means	0.56	0.40	0.09	0.43–0.70
Mean from total *N* and *T*	0.55	0.59	NA	0.36–0.63

The shape of the posterior distribution of *R* results from the interaction of the shapes of the distributions of *T* and *N* (which are near normal for all populations) and the binomial likelihood. The likelihood values (weights) of each value of *R* in the posterior are the values assigned to the value of *N* evaluated for each value of *R*. Values of *R* near the upper end of the prior distribution will have high likelihood values only for values of *T* at the upper range and *N* at the lower range of their respective distributions, and these combinations constitute only a very small proportion of the sampled joint parameter space.

Total catch

The posterior modal value of the estimated catch for the four river-specific populations ranges from 37 700 for the Stillaguamish to 91 300 for the Nooksack. For the remainder of Puget Sound rivers and streams, the modal catch was 109 000. The central 90% of the posterior distributions ranges from 31 100 to 46 600 for the Stillaguamish to 81 700 to 113 500 for the Nooksack, and from 89 400 to 134 500 for the remaining streams. For Puget Sound as a whole, the central 90% ranges from 306 700 to 452 000.

Harvest rate

The posterior distributions for all five populations are virtually identical. They span the entire width of the prior distribution, but approximate a negative exponential distribution in shape with posterior probabilities steadily declining from left to right and modal values that are essentially at the lower (left) limit of the prior distribution. The modal values are approximately 1.5 times more probable than the value of the upper limit. Modal values of R range from a low of 0.31 for the Skagit to a high of 0.6 for the Nooksack. Central 90th percentile distributions range from 0.31 to 0.58 for the Skagit to 0.61 to 0.88 for the Nooksack. For the total Puget Sound population, the central 90th percentile spans the range from 0.36 to 0.63 when calculated on the summed total catch and summed total run size estimates for the five populations.

Taken together with the fact that the posterior distributions of N are well within the limits of their respective prior distributions, the posterior distributions of R show that the span of the priors is informative, even though the shape is uninformative. It therefore suggests that the upper bounds of the priors on R are appropriately large; that is, it is unlikely that the true harvest rates were larger. To the extent that this is true, it is therefore unlikely that the true run sizes are smaller than the lower end of the posteriors of N. Consequently, the majority of the uncertainty that remains concerns how low the harvest rates and how large the run sizes may have been.

Run size

The posterior modal value of N ranges from 73 700 for the Stillaguamish to 153 000 for the Snohomish and 185 000 for the remainder of Puget Sound streams. The 5th percentile of the posterior distributions ranges from 51 700 (Stillaguamish) to 114 000 (Snohomish) and 148 000 for the remainder of Puget Sound. Thus, the probability is 0.95 that the respective run sizes of these populations are greater than these values. For all of Puget Sound, the 5th percentile value is 485 000 and the 95th percentile is 930 000.

Comparison of historical with contemporary run size

The relevant data for the comparison of 1895 and contemporary Puget Sound run sizes are presented (Tables 2–4). The numbers are sobering. For the recent 25-year period from 1980 to 2004, the average annual total Puget Sound run size is 21 700. For the 5-year period 2000 to 2004, the average annual total is 15 500. The posterior modal estimate of the total Puget Sound run in 1895 is 621 700. The posterior 5th percentile estimate is 485 000. Our posterior modal historical estimates are 29 and 40 times larger, respectively, than the 25- and 5-year contemporary averages. The posterior 5th percentile historical totals are 22 and 31 times larger.

Compared with the average run sizes over the recent 25-year period between 1980 and 2004, posterior modal run sizes from our historical estimates for individual rivers are 12 (Skagit) to 67 (Stillaguamish) times larger. The lower 5th percentile of the posteriors of our estimates are 10 (Skagit) to 50 (Stillaguamish) times larger.

Expressed in terms of FKM, the value averaged over the average total run size for all Puget Sound streams is 3.1 for the recent 25-year period and 2.2 for the recent 5-year period. The value of FKM corresponding to the posterior modal estimate of the total 1895 run size (621 700) is 59 and for the posterior 5th percentile estimate (485 000) is 46 (Fig. 4).

For the four individual rivers, FKM values range from 2.31 for the Stillaguamish to 7.12 for the Skagit for the recent 25-year averages and from 1.24 for the Stillaguamish to 5.52 for the Skagit for the recent 5-year averages. Comparable FKM values for the 1895 estimates range from 59 for the Skagit to 139 for the Nooksack based on our posterior modal run size values and from 48 for the Skagit to 110 for the Nooksack based on our posterior 5th percentile run size values (Fig. 4).

Discussion

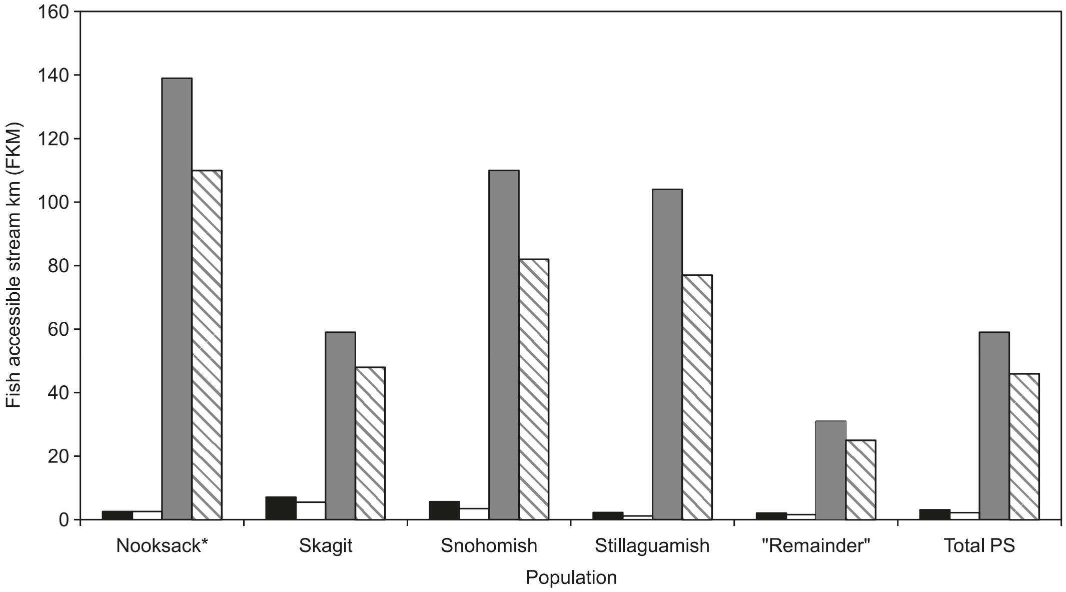
The point of this paper was to provide, from available historical data, a credible estimate of the winter steelhead return to Puget Sound streams just prior to the turn of the 20th century. We argue that our methodology and results do provide such a credible estimate, and furthermore, they reveal a great discrepancy between the return of 110 years ago and returns of today. Those familiar with winter steelhead life history, ecology, and fishery management could probably list a number of factors that could have contributed to this discrepancy and could devise ways to estimate how much of the discrepancy each factor could have accounted for. That was not our objective in this paper. Even so, we did examine two such factors, namely stream habitat loss between periods and, in an assessment made during review, marine survival differences between periods. These two factors are discussed below.

Stream habitat loss

The difference between the estimated 1895 run sizes and the recent abundance of Puget Sound steelhead far exceeds even the most liberal estimates of the amount of stream habitat lost during the intervening 110 years. Dramatic loss of the productivity of Puget Sound steelhead must have occurred, and this loss would appear to dwarf the quantitative loss of habitat. For example, we estimate a maximum loss of one-third (33%) of all of the linear stream habitat that was accessible to adult steelhead in each river and stream system in Puget Sound in 1895. Yet this loss was paralleled by a 25-fold (2500%) or greater loss in abundance. Whereas the current length of streams accessible to adult steelhead throughout Puget Sound is no less than two-thirds of what it was in 1895, abundance is at most 4% of what it was in 1895 and most likely is smaller than that (in the neighborhood of 2%).

Our estimates of habitat availability measured as length of stream accessible to returning adult steelhead is a rough metric that we employ for want of a more refined, accurate measure. This metric does not account for changes in the quality of the available stream habitat. At this stage of the

Fig. 4. Fish-per-accessible-stream-kilometre for recent average and estimated 1895 abundance of Puget Sound steelhead. Black bars: recent 25-year average; open bars: recent 5-year average; grey bars: 1895 posterior mode; hatched bars: 1895 posterior 5th percentile.



analysis, however, we view this as a strength because it indicates that the severe reduction in the abundance of Puget Sound steelhead must be due primarily to a loss of capacity of the available habitat. This loss may reduce the carrying capacity of freshwater habitat directly through loss of suitable habitat or indirectly through changes in conditions that affect population productivity (via affecting growth and survival of early life stages). It remains to be determined to what extent this loss of productivity is due to changes in the physical and ecological conditions of freshwater habitat and which components of the steelhead life cycle may be most affected.

To provide further perspective on these estimates, we considered data for steelhead in the Situk River in southeast Alaska. Specifically, we examined data from 1952 based on weir counts that constituted a near-complete enumeration of the 1952 steelhead run (Bain et al. 2003). This run occurred at the end of a period of 12–15 years of rebuilding (two to three generations) that followed the cessation of efforts directed at eradicating steelhead in the Situk. During this rebuilding period, sport fishing and incidental commercial harvest was minimal (estimated annual harvest rate less than 8%), and spawning and rearing habitat conditions were as close to undisturbed as any stream or river in North America in the 20th century for which comparable data exists. The estimated run size ranges between 25 000 and 30 000 for the Situk at that time (Bain et al. 2003), and the best estimate of total stream kilometres accessible to adult steelhead is 100 km (Thedinga et al. 1993; B. Marsten, Yakutat Area Fish Biologist, Alaska Department of Fish and Game, P.O. Box 49, Yakutat, AK 99689, USA, personal communication 2009). This results in a range for FKM of 250–300, a range of values substantially greater than any of the values from our estimates for Puget Sound rivers in 1895, all of which are less than 150 FKM (Fig. 5).

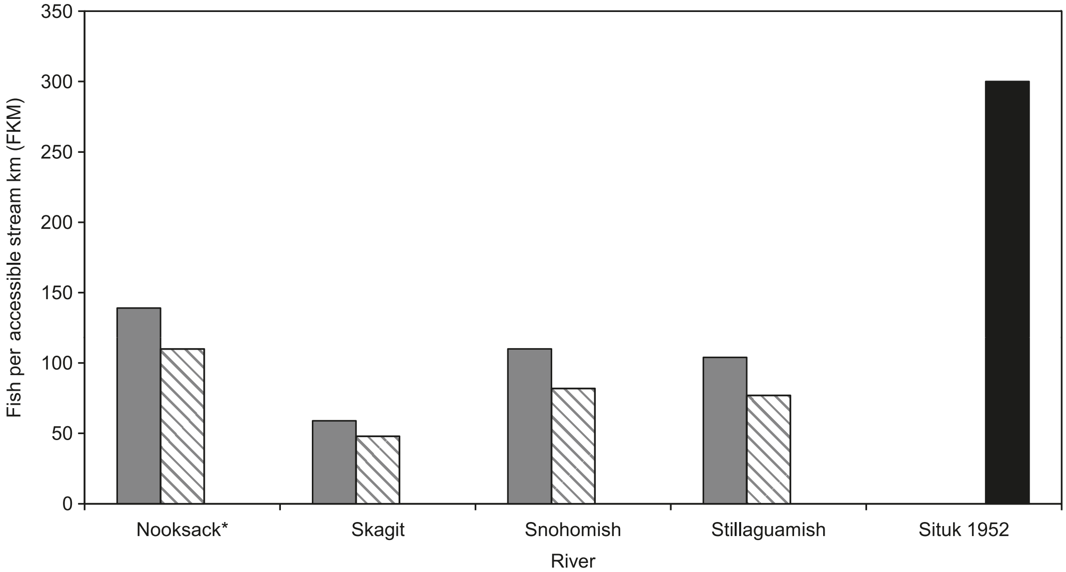
The Situk is a low-gradient, lake-controlled tundra river and might thus be thought to be unrepresentative of the productive potential of Puget Sound rivers. However, while it is clearly geomorphically different than most streams and rivers in the Puget Sound lowlands, it is arguably more relevant to the consideration of the inherent productive potential for steelhead of Puget Sound rivers than might first appear. The majority of large rivers in Puget Sound prior to being modified by Euro-American activities had extensive low-gradient floodplains with heavy loadings of large wood, braided channels, and vast wetlands (e.g., Bancroft 1890; Collins and Sheikh 2004; and Collins 2008) that created complex, low-gradient riverine habitats with rearing and spawning conditions that were likely not much different from the Situk. Given these historic conditions, we suggest that the Situk data provides a helpful perspective on the FKM values for Puget Sound that are associated with our 1895 estimates.

Potential importance of marine survival between periods

We have not speculated on possible differences in juvenile steelhead survival in the ocean between the period affecting the recruitment of the 1895 steelhead run and the period between 1980 and 2004. There are several reasons for this. First, we believe it unlikely that the 25-fold difference in abundance between the two periods that we have estimated could be accounted for primarily by differences in ocean survival. Differences in stock-specific smolt-to-adult survival of steelhead over a 20- to 30-year time span that have been recorded appear to be on the order of fourfold (Ward 2000). But even a 10-fold difference would not account for the discrepancy we have identified.

In this connection, it is relevant to note that early ocean survival of steelhead does not appear to exhibit as strong or as consistent a correlation with indices of ocean productivity such as the Pacific Decadal Oscillation (PDO) as do coho salmon *Oncorhynchus kisutch*. Second, to the extent that ocean survival of steelhead does follow the pattern of coho, it is of interest to note that the ocean conditions in the decade leading up to the 1895 Puget Sound steelhead run as indexed by the PDO appear to have been unfavorable. Biondi

Fig. 5. Fish-per-accessible-stream-kilometre for four major Puget Sound rivers estimated 1895 abundance and for Alaska's Situk River in 1952. Grey bars: 1895 posterior mode; hatched bars: 1895 posterior 5th percentile.



et al. (2001) reconstructed the PDO from 1991 back to 1661 based on the analysis of tree rings (dendrochronology) of bigcone Douglas-fir (*Pseudotsuga macrocarpa*) and Jeffrey pine (*Pinus jeffreyi*) from sites in southern California and northwestern Mexico. The reconstructed series correlated well with the PDO calculated directly by Mantua et al. (1997) for the period between 1900 and 1991 (correlation coefficient = 0.49, $P < 0.001$). A subsequent analysis of five published proxy records of North Pacific climate variability, including the Biondi et al. (2001) study, arrived at similar conclusions (Gedalof et al. (2002). During the decade from 1885 to 1894 that spans the period of juvenile recruitment to the 1895 adult run, the reconstructed PDO of Biondi et al. (2001) was consistently positive. A positive PDO correlated with poor ocean survival conditions for juvenile salmonids from southern British Columbia (Hare et al. 1999). The reconstructed series was also positive from 1977 to 1989 in accordance with the PDO as reported by Mantua et al. (1997), and which spans the first half of the 1980 to 2004 period. This suggests, but of course does not prove, that ocean conditions affecting steelhead recruitment to the 1895 run were not hugely different from those experienced in the recent past.

Differences between our estimate and that of Hard et al. (2007)

Our historical run size estimate is considerably larger than the 327 522 to 545 997 fish estimate prepared by Hard et al. (2007) for NOAA Fisheries' most recent status review of Puget Sound steelhead, even though both estimates are based on the same 1895 commercial harvest data set. There are two essential reasons for this. First, Hard et al. (2007) assumed that the average Puget Sound steelhead weighed 5.4 kg (12 lb) based on a reported average size range of 3.6 kg (8 lb) to 6.8 kg (15 lb), with an extreme of 11.3 kg (25 lb) (Rathbun 1900). Our deeper analysis of the available historical evidence indicated that this average mass was too high and should most likely lie within the bounds of 3.2 kg (7 lb) and 4.3 kg (9.5 lb). Second, we argue that the unreported catch of winter steelhead was much larger than Hard et al. (2007) suspected. Our analysis of available historical information indicated that the recorded commercial catch of steelhead likely only represented between one-half and two-thirds the actual catch in river basins where Native American subsistence fishing took place and also where agriculture was a dominant Euro-American settlement activity. Accordingly, we argue that the total harvest rates on the runs were likely to have been much higher than Hard et al. (2007) assume.

With regard to Euro-American settlement activity, our historical research revealed that staggering numbers of salmon and steelhead were speared, pitch-forked, snagged, and trapped at virtually every tributary, rill, and brook at spawning times by settlers who used the fish by the wagonload for fertilizer and livestock feed (Local Committee of Pioneers 1906; Jeffcott 1949; Edson 1968). The need for fertilizer was likely linked to the low soil nutrient levels in river valley areas previously forested with old growth trees. Clark (1970, p. 35) explains that the denuded forest soil was "acidic, sandy, and lean in minerals, good for fir and cedar but terrible for food crops. Without fertilizers which few people could obtain, it might yield at best a few grubby vegetables when cultivated with prayer and desperation." However, fertilizer was readily at hand in the streams, and settlers quickly learned to use the abundant spawning runs of anadromous fish (salmon in fall and steelhead in winter–spring) to build soil productivity prior to each planting.

Although Native American subsistence fishing was much reduced by 1895 from levels that occurred prior to Euro-American settlement, the schedule of this activity was much the same: salmon in the fall and steelhead in winter and spring. The rather considerable body of anthropological and ethnohistorical literature available for the Puget Sound region makes it clear that Puget Sound tribes did capture and utilize winter steelhead, and indeed these fish were prized by the Indians (e.g., Stern 1934; Smith 1940; Suttles 1974), even though much time was also spent in the longhouses in winter engaged in story-telling, ceremonies, and feasting (Schalk 1977).

Historical commercial run-up to 1895 data set and the 70–30 split

It is worth noting that the 1895 commercial catch for the "remainder of Puget Sound" represents only 27% of the total, yet includes several large rivers in central and south Puget Sound: the Green, Puyallup, and Nisqually. Whether or not these rivers in particular had been heavily commercially fished prior to the late 1890s is difficult to determine from the available historical record. Puget Sound commercial fishing began more than 40 years prior to 1895 (1853), with increasing layers of commercial, subsistence, and agricultural harvests that went unrecorded until record keeping began in 1889. The pattern of development of settlement and commerce that included fishing moved predominately in a south-to-north direction. Commercial fishing in particular necessitated the arrival of railroads, which also developed in a south-to-north direction in conjunction with population growth. By 1890, the two Seattle–Tacoma area counties had a total population of 115 000 people, whereas the most populated north Puget Sound county had less than 19 000. Seattle and Tacoma were the major early fishing centers that peaked prior to any record keeping. By 1895, Tacoma was no longer even considered a fishing center. Consequently, for whatever reason, by 1895 the contribution of the large central and south Puget Sound rivers to the commercial steelhead catch was considerably smaller than the four large northern rivers. This is another reason that our estimate of the total Puget Sound run size in 1895 is conservative and under-represents the historic productive potential of Puget Sound rivers.

Relevance for recovery planning

The magnitude of the decline identified by our estimates of 1895 run sizes appears well out of proportion to the loss of habitat available to steelhead, as measured by our rough metric for habitat quantity. There is a considerable amount of stream habitat throughout Puget Sound that remains accessible to adult steelhead. Yet for reasons that remain to be identified or understood, the available habitat lacks either the capacity to hold the numbers of juveniles that it did around the turn of the 20th century or the conditions that enabled it to produce large numbers of healthy individuals that would survive to outmigrate as smolts.

Recovery planning for Puget Sound steelhead will need to identify and evaluate credible hypotheses about the causes of the severe decline in habitat capacity and productivity that is identified by our estimates of turn-of-the-20th-century abundance. Assessment of this loss is necessary to identify appropriate abundance targets for recovery that will insure the persistence of a delisted ESU. Clearly, there have been numerous changes to the environment occupied by Puget Sound steelhead as well as to the fish themselves. Interactions with hatchery conspecifics, reduction in the magnitude of runs of Pacific salmon, and simplification of life history components such as reduction or elimination of repeat spawning, in addition to possible changes in the magnitude and (or) pattern of marine survival, are all likely contributors that will have to factor into a comprehensive understanding of the decline in overall abundance that our analysis has indicated. There is some cause for optimism here in that the comparatively small amount of physical stream habitat lost over the past century relative to the magnitude of population decline suggests that recovering substantially larger wild population sizes may clearly still be in the cards.

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Appendix A

For the equation used to calculate the binomial likelihood (eq. 1), we begin by stating full factorial version of the binomial likelihood:

$$\text{(A.1)} \qquad P(T|N,R) = \frac{N!}{T!(N-T)!} \cdot T^R \cdot (N-T)^{(1-R)}$$

where $T = C{\cdot}(1 + U)/M$, C is the reported 1895 commercial catch in pounds, U is a value for the unreported catch (in pounds) as a proportion of the reported commercial catch drawn randomly from the prior distribution of U, and M is a value for the average mass of steelhead in the run drawn randomly from the prior distribution of U.

In SWL, the likelihood is calculated in natural log space (ALOG). Equation A.1 must therefore be translated into natural log space. This requires the use of the logarithm of the gamma function (LGAM) to handle the factorials. We define the following:

FN = N + 1.0
FT = T + 1.0
FF = FN – FT + 1.0

GN = LGAM(FN)
GT = LGAM(FT)
GF = LGAM(FF)

The log-likelihood is then calculated from

$$\text{(A.2)} \qquad (\text{GT} - \text{GT} - \text{GF}) + T \cdot \text{ALOG}(R) + (N - T) \times \text{ALOG}(1 - R)$$

As described in the text, eq. A.2 is calculated for each of 10 000 000 sets of random values sampled from the prior distributions of N, R, U, and M, and each set is then weighted by the likelihood value calculated for the set. Histograms and posterior summaries of selected parameters of interest are derived from these weights. Derived parameters, such as T, are also derived from these weights in a straightforward way (T, for example, using eq. 2 as explained in the text).